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Diurnal and seasonal stomatal behaviors of rice plants grown in controlled environment

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Abstract. The diurnal and seasonal changes of stomatal movement of rice (*Oryza sativa* L.) plants were studied in the controlled environment. The results showed that the diurnal patterns of stomatal behavior were shown in the seasonal fashions. A decreasing trend of stomatal diffusive conductances were observed in the vegetative growth phase followed by a dramatic increase of conductance began at Leaf 16 stage, which is concurrent to the panicle formation period. Stomatal conductances were dropping after heading as plant aged. Such phenomenon can be clearly discerned by plotting the data at 0800, 1400 and 2000 h. It is suggested that the indicated behavior of stomata may be a compromise of its own economy by optimizing photosynthetic capacity in the sacrifice of transpiration loss because of the elevated demand of photosynthetic assimilates for reproduction.

Key words: *Oryza sativa* L., Stomatal movement, Diurnal, Seasonal, Controlled environment.

水稻葉片氣孔在控制環境下每日週期性及季節性之變化

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摘要：本文旨在觀測水稻（*Oryza sativa L.*）葉片氣孔在控制環境下每日週期性及季節性之變化。結果顯示，水稻葉片在恆常狀況下具有週期性之氣孔運動，且此種每日週期之行爲具有季節性變異。在營養生長期間，氣孔傳導度隨株齡（以葉齡表示）之增加呈現下降趨勢，直至第16葉齡期間突然明顯地升高。由於此時期恰爲穗形成期，故此一現象可能爲稻株追求高光合成需要所作之自身調節。氣孔傳導度自抽穗開花後便逐漸降低。

關鍵語：水稻、氣孔行爲、每日週期性、季節性、控制環境。

INTRODUCTION

The transport of water through the soil-plant-atmosphere continuum is determined by the balance between plant influx and efflux. Water loss from the plant via transpiration is an inevitable consequence of the need to open stomata to facilitate carbon dioxide assimilation. The central role of stomata, therefore, is to regulate water vapor and carbon dioxide exchange through the control of its aperture and hence of diffusive conductance (inverse of resistance).

As plant ages, many features of leaf structure and physiological functions are changed. Stomatal conductance varies with leaf age (Constable and Rawson 1980). Changes of stomatal behavior may also occur in response to the progressive changing in physiological status when plant develops (Jonses 1979, Turner and Heichel 1977). A number of environmental variables can exert their effects on stomatal behavior at anytime so that the resultant stomatal aperture is an expression of the interaction of these variables plus internal modifications.

Upon the early minutes of light, stomata open gradually before reaching an optimum which is maintained during the greater part of the day known as steady state opening. Guard cells then close at night to complete one cycle showing rhythmic behavior with a repeated frequency of approximately 24 hours under normal environmental conditions (Martin et al. 1983). Although stomata response may differ in species, such responsiveness confers a substantial advantage for organisms to response in time to external conditions and to allow a particular response to be synchronized with advantageous environments. It is not well-known, however, the seasonal changes of stomatal behavior to the physiological status and plant age of plant, especially in rice plants and under controlled environment. The variation of diurnal pattern of stomatal diffusive conductance as plant advances is also not fully understood. Thus, studies conducted under controlled environment are needed to provide information on the diurnal and seasonal stomatal behaviors and to show plant adjust its stomatal aperture as a means to synchronize the development requirement. Such investigation is especially interesting in the absence of irradiance variation and water deficiency under constant daily humidity difference.

In this study, changes of stomatal movement of rice plants as a function of time and leaf stage (plant age) were measured under controlled-environment. The physiological implications of regulation of stomatal behaviors were discussed.

MATERIALS AND METHODS

Plants of rice variety Lemont were grown in opaque plastic containers (.25 m diameter, .20 m height, 0.049 m^2 surface area) filled with fritted clay. Three plants were grown per pot, with even space, and irrigated with nutrient solutions (see Yang

and Heilman 1990). Plants were irrigated in excess twice a day, early morning and late afternoon, to keep the soil saturated. To avoid salt accumulation, the pots were flushed with distilled water, every 7 days during the vegetative growth phase and every 3 days during the reproductive growth phase. The pots were plugged in the center so that extra water was drained from the soil after irrigation.

The rice plants were grown as groups in a growth chamber with circulated ambient air (day/night temperatures 30 C/20 C; relative humidity 55-70%/90-100%; CO_2 concentration 330-430 ppm). The daylength was 12 hours (0800-2000 h) with a PPFD (photosynthetic photon flux density) of about 680 μmole $m^{-2}s^{-1}$. Wind speed was about 0.8 ms^{-1}. They were rotated periodically to ensure uniformity within the chamber.

The leaf stage (plant age) was assessed by the emergence of the primary leaf on the main culm (Yoshida 1981). Heading stage (H) is defined as from the first day to the 7th day from heading (one week); the R – 1 stage is the time period from the 8th to the 14th day from heading, and so on. Stomatal (leaf) diffusive resistance was measured in the middle portion of the youngest fully expanded primary leaves by a porometer (MK3, Delta-T Devices, England). For diurnal data, the first measurement was taken at 0800 h, the onset of photoperiod, and the measurements were continued every two hours until 2000 h, the end of daytime hours. Stomatal conductance, the inverse of stomatal resistance, was used throughout this study. The mean values were taken from the averages of each group; at least four groups for each mean value.

RESULTS

Basically, a diurnal pattern of stomatal behavior was shown in the seasonal fashion (Figs. 1-3) during the life span of rice, even under controlled environment. This behavior is more discernable as shown in Fig. 4. Although temperature and irradiance were constant in the growth chamber during the day, stomatal conductance was generally higher in the middle portion of the photoperiod. Greatest diurnal variations occurred early in the vegetative stage (Leaf 5 stage) and in the reproductive growth stage (beginning from Leaf 16 stage). These results, with others (Taniyama et al. 1987), support the viewpoint that stomatal movement is one of the endogenous controls (Martin and Meidner 1971, Martin et al., 1983), also known as circadian rhythms. This periodicity evolved since the most dominant environment change on the earth is the alteration of day with night (Brady 1979).

A decreasing trend of stomatal conductance pattern was observed, from Leaf 5 through Leaf 15 stage (Fig. 4). This phenomenon may be the result of an accumulated wax barrier and polysaccharide substances in guard cells, as well as leaf layers, as the plant ages (Palevitz 1981, Willmer 1983). These barriers would

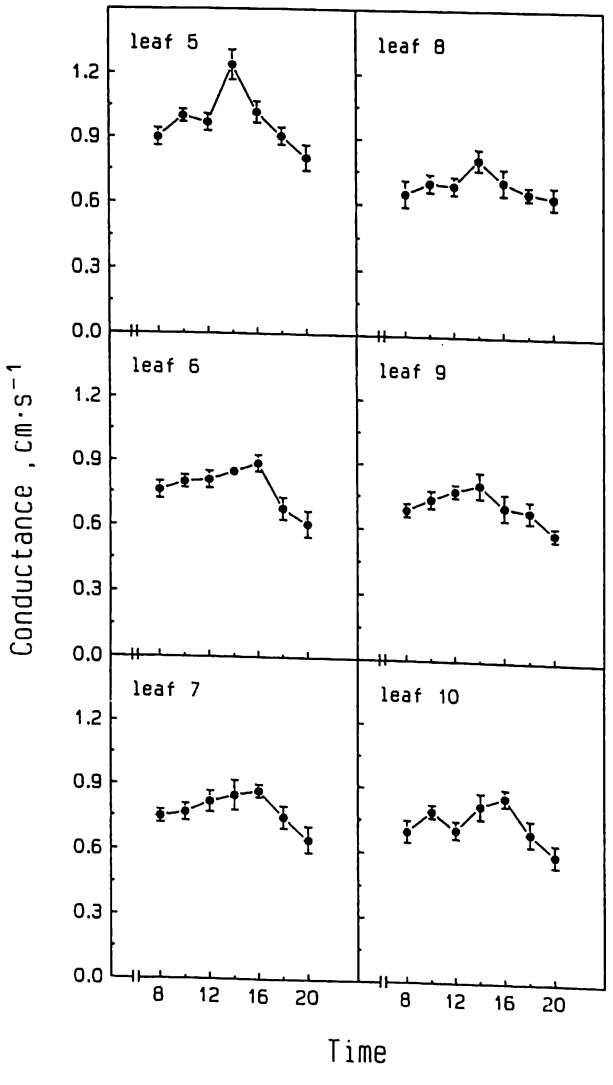

Fig. 1. Stomatal conductances of primary leaves 5-10 at the Leaf 5 to Leaf 10 stages, respectively. The measured primary leaves were the youngest fully expanded leaves. Standard deviation is included.

impede evaporative water loss as the amounts of water vapor tend to increase with the increase of plant canopy. Changes of the need of photosynthetic assimilates from the individual leaves may also involve, as more leaves emerge and therefore reduce photosynthesis burden (photosynthetic rate per unit leaf area) of each single leaf of plant canopy. The reduction of photosynthetic rate may alter stomatal aperture and hence diffusive resistance.

However, it is worth noting that a dramatic increase of stomatal conductance began at Leaf 16 stage, more than 60% (Figs. 2 and 4), concurrent to panicle formation period. This may be a compromise of its own economy by optimizing photosynthetic capacity in the sacrifice of transpiration loss because of the elevated

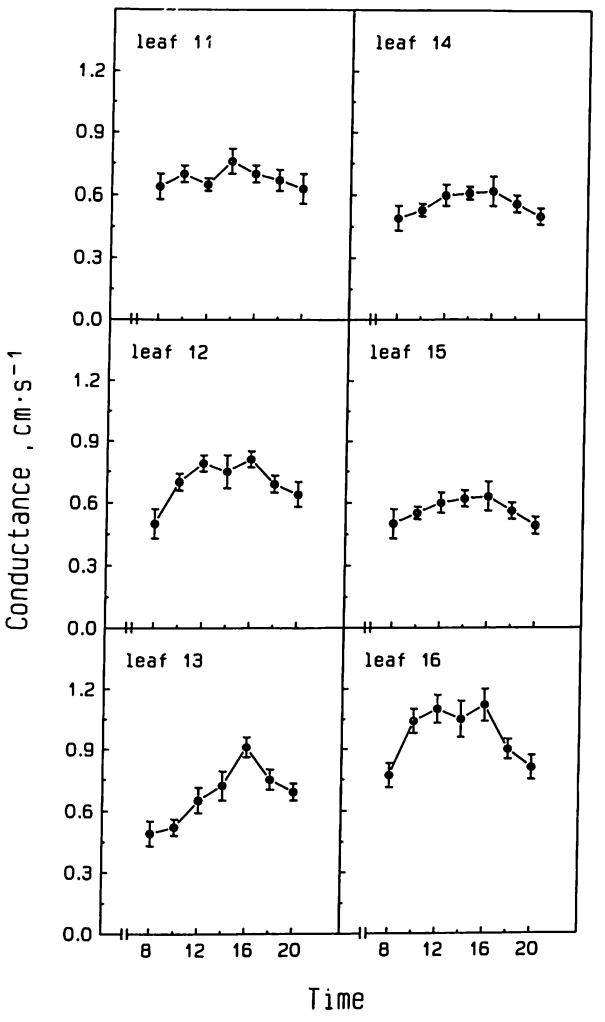

Fig. 2. Stomatal conductances of primary leaves 11-16 at the Leaf 11 to Leaf 16 stages. The measured primary leaves were the youngest fully expanded leaves. Standard deviation is included.

demand of photosynthetic assimilates for reproduction. The decrease of conductance after heading is no surprise since the senescence of plant canopy was in progress.

Two fundamental processes of stomata are illustrated: the versatile performance and the development of their ability to adjust their opening and closing (Martin et al. 1983). By controlling these two processes, stomata movements seem to perform an essential function in contributing to production efficiency in the life cycle of rice. More studies in the area of stomatal physiology and guard cells response to environmental stimuli, however, is needed to further elucidate stomatal response.

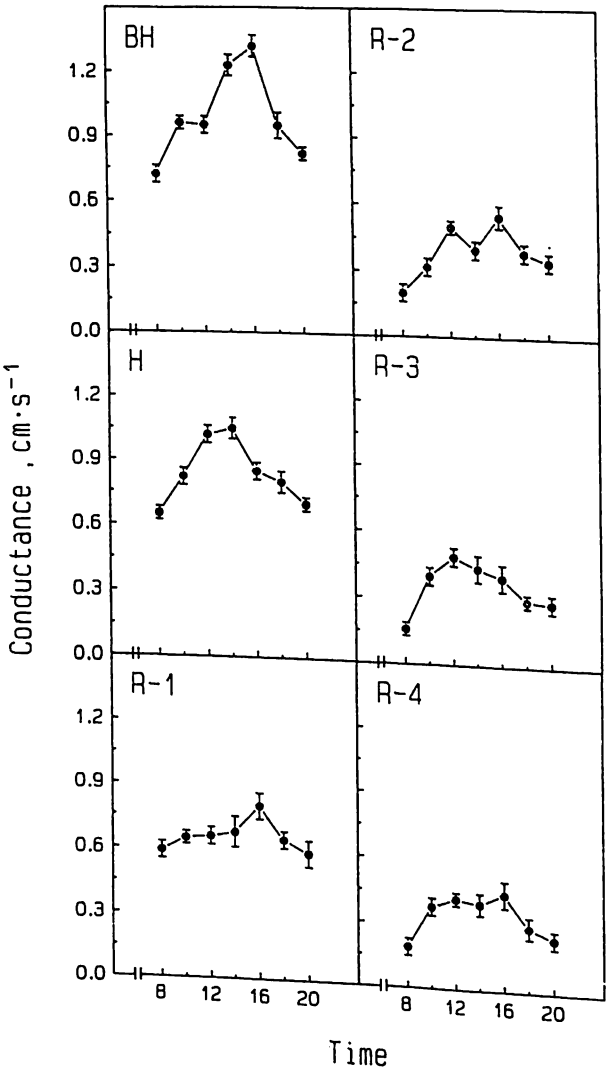

Fig. 3. Stomatal conductances of primary leaf 17 at the Heading to R-4 stages. The measured primary leaf was the uppermost fully expanded leaf. Standard deviation is included.

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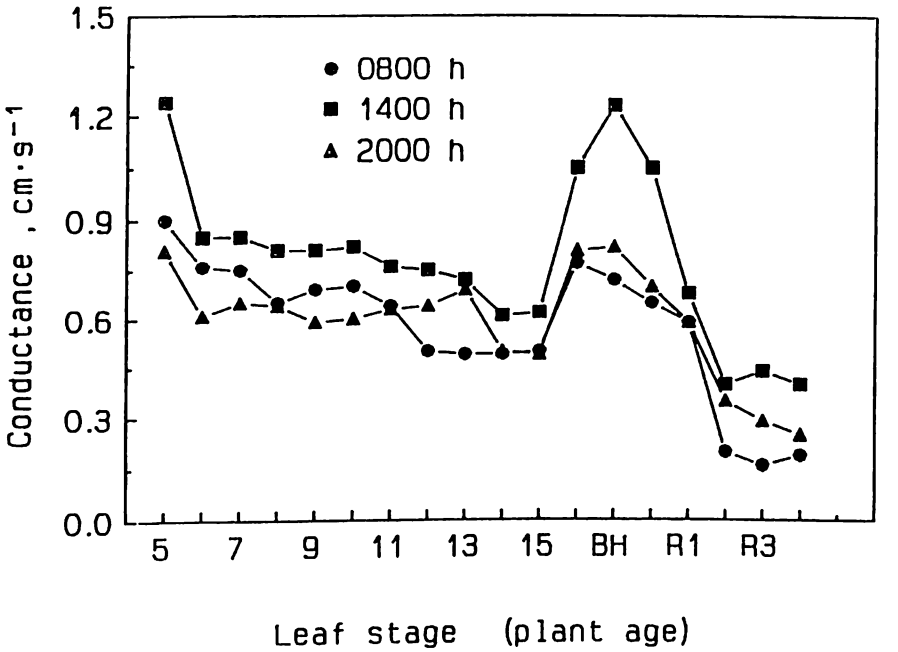

Fig. 4. Stomatal conductances at 0800, 1400 and 2000 h as a function of leaf stage (plant age) under controlled-environment conditions. BH: before heading period (7 days before heading to heading), H: heading stage.

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